ARBORAMOSA SEMICIRCUMTRACHEA, AN UNUSUAL LATE TRIASSIC TREE IN PETRIFIED FOREST NATIONAL PARK, ARIZONA, USA

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ABSTRACT – A petrified stem from the Late Triassic Chinle Formation in Petrified Forest National Park, Arizona has a fluted wood surface and spirally distributed branch stubs emerging from within fusiform depressions, giving the stem a coarsely braided appearance similar to some modern *Juniperus* trees. In cross section, the secondary xylem exhibits growth interruptions and comprises jumbled radial files of thick-walled, rounded and semi-rounded tracheids, and infrequent, short, homogeneous, uniseriate rays. Circular, equidiameter, spatially separated bordered pits occur as linear, uniseriate chains on diagonal and tangential as well as radial walls of the 10-mm-long tracheids. The ray cells have distantly spaced taxodioid, rarely cupressoid, crossfield pits in their thin radial and horizontal walls. Morphological and tracheidoxyl phenotypes of the stem are indicative of a new genus and species, a transient genetic anomaly within a landscape dominated by trees having araucarian wood.

Keywords: Arizona, Chinle Formation, Upper Triassic, conifer, Araucariaceae

INTRODUCTION

PETRIFIED WOOD contains information about form, size, ecophysiological adaptations and fundamental biological processes which once occurred in the living woody plant. Fossil woods can readily be found in the Upper Triassic Chinle Formation of Petrified Forest National Park (PEFO), northeastern Arizona, USA. However, only nine fossil species having secondary xylem have been identified in PEFO, only five of these nine had more than a centimeter of secondary xylem, and no new log-sized species has been described since 1941 (Table 1). Moreover, most of the descriptions of petrified wood in PEFO are based on just one or two specimens and cannot be described as comprehensive. This rudimentary state of knowledge about the petrified woods in PEFO is unfortunate, as paleobotanists recognized more than a century ago that "any description of fossil wood which is to be of use in the future must include an exhaustive analysis of all the characters, both absolute and relative, which have not been proved to be purely fanciful" (Barber, 1898). Counterbalancing the present dearth of information is the responsible management of PEFO woods for ongoing investigation.

Petrified logs of a conifer referred to as *Araucarioxylon arizonicum* Knowlton (1888) are found throughout PEFO as the largest fossils (Table 1). In addition to *A. arizonicum*, several other Triassic *Araucarioxylon* species have been described in North America (Knowlton, 1919). However, as explained by Bamford and Philippe (2001), the name *Araucarioxylon* (*sic*, originally *Araucaroxylon* – Kraus, 1870) is actually invalid according to the rules of the International Code of Botanical Nomenclature (Greuter et al., 1999), and many tracheidoxyls (i.e., permineralized fragments of pycnoxylic secondary xylem – Creber, 1972) formerly ascribed to that

genus have been reclassified into *Agathoxylon,* a genus created by Hartig (1848). Further research is needed to decide if *A. arizonicum* should be emended to *Agathoxylon* or another genus, but photomicrographs by Daugherty (1941) of putative *A. arizonicum* wood (from PEFO) are not in good agreement with the original description of *A. arizonicum* wood (also from PEFO) made by Knowlton (1888). It seems probable that some of the large logs in PEFO are species different from *A. arizonicum*.

Although they are smaller and not nearly as abundant as those of *A. arizonicum*, logs of *Woodworthia arizonica* Jeffrey, 1910 and *Schilderia adamanica* Daugherty, 1934 are the type species of two monotypic genera found only in the Black Forest Bed of PEFO, usually in close proximity to logs of *A. arizonicum*. As indicated in Table 2, *W. arizonica* has secondary xylem similar to that of *A. arizonicum* and, like the latter, is thought to have been a conifer, but it is readily distinguished by having numerous short shoots embedded throughout its wood (Jeffrey, 1910; Daugherty, 1941; Creber and Ash, 2004). *S. adamanica* has manoxylic wood containing conspicuously wide herring-bone rays similar to those in the secondary xylem of the extant genus *Ephedra* (Gnetophyta, Ephedraceae), making it entirely distinct from both *A. arizonicum* and *W. arizonica* (Daugherty, 1934, 1941).

Dadoxylon chaneyi (Daugherty, 1941) is a fourth kind of petrified wood in PEFO. However, for similar reasons to those invalidating *Araucarioxylon*, the name *Dadoxylon* is not acceptable within ICBN rules (Bamford and Philippe, 2001). *Dadoxylon* has a history of being applied rather liberally to a heterogeneous group of woods having araucarian features in Pityaceae, Cordaitaceae and Coniferae (Darrah, 1939). In addition, since the early 20th century paleobotanists have shown a tendency to use *Dadoxylon* to refer to Paleozoic

woods and *Araucarioxylon* to refer to Mesozoic or more recent woods (Darrah, 1939), although such usage based on geological age was not accepted by all (Seward, 1917). *Dadoxylon* as originally used (Endlicher, 1847) required the presence of large diameter pith, a characteristic of Cordaitales (Seward, 1917; Arnold, 1947; Lepekhina, 1972; Stewart, 1983), whereas *Araucarioxylon arizonicum* as a conifer has small diameter pith (Ash and Savidge, 2004). The specimen described by Daugherty (1941) had a non-discoid pith 16 mm in diameter, surrounded by secondary xylem *c.* 2 cm in radial thickness. As noted by Seward (1917), a discoid pith although common is not an invariable attribute of stems closely allied to the Cordaites. In view of the above problems, we suggest that *Dadoxylon chaneyi* (Daugherty, 1941) be re-examined for its taxonomic affinity.

A fifth kind of wood that was collected a short distance west of the PEFO park boundary is *Lyssoxylon grigsbyi* Daugherty (1941). Daugherty (1941) interpreted *L. grigsbyi* to be a cycadeoid (family Williamsoniaceae) on the basis of a fragment of wood with attached cycad-like bark. However, subsequent research indicated the fossil to be a true cycad (Gould, 1971; Vozenin-Serra, 1979). *Lyssoxylon grigsbyi* has spiral-banded secondary-xylem tracheids, well-spaced circular bordered pits and both uni- and multi-seriate fusiform rays (Table 2). Another cycad, *Charmorgia dijolli* Ash (1985) having a short stubby stem, large diameter pith and a narrow width of araucarian xylem, also is known (Table 1).

The fossil tree stem described here as *Arboramosa semicircumtrachea* n. gen. et n. sp. occurs in the Crystal Forest of PEFO and has phenotypic features distinguishing it from *A. arizonicum*, *W. arizonica*, *S. adamanica, D. chaneyi* and *L. grigsbyi* (Table 2). Its stem and tracheidoxyl appear not only to be unique in relation to known petrified logs in PEFO but distinct from all known fossil woods. The integrated morphological/anatomical phenotype points to the tree having been a transitional species, possibly a distant ancestor of trees like our modern junipers.

PREVIOUS INVESTIGATIONS

The first plant fossils to be collected for scientific study from the region that is now contained within the boundaries of Petrified Forest National Park were pieces of petrified wood. As noted by several authors (e.g., Knowlton,1888; Daugherty, 1941; and Ash, 1972), they were collected in 1853 from the Black Forest Bed of the Chinle Formation in Lithodendron Wash in the northern part of the park by members of the U.S. Army Exploring Expedition led by Lt. A. W. Whipple. Tracheidoxyls collected at that time by the German traveler Baldwin Möllhausen were given to the German paleobotanist H. R. Göppert who reported that they were of the Abietina and Araucaria types (Göppert, 1858). In the same book, Göppert

also named one specimen of wood *Araucarites möllhausianus*, but he neglected to describe the species and the name is therefore considered a "nomen nudum" (Ward, 1900, p. 317). Additional specimens collected in the same area by other members of the expedition were turned over to the American geologist W. P. Blake (in Whipple, 1855) who reported that the wood structure was "distinctly" preserved in them, but Blake did not identify the woods. In 1879 two large sections of a log were collected from the Black Forest Bed in the same general area by U.S. Army soldiers under the command of Lt. J. T. C. Hegewald and shipped to the Smithsonian Institution in Washington, D.C., for exhibit (Swaine and Hegewald, 1882). That log was later studied by the American paleobotanist Frank Knowlton who, in 1888, described the tree as *Araucarioxylon arizonicum*. Thereafter, fossil wood having the gross morphology of *A. arizonicum* has been reported from many Upper Triassic localities in the southwest, but the internal anatomy of the wood has only been studied by a few of the later workers. Daugherty (1941) published three photomicrographs of "*Araucarioxylon arizonicum*", but he merely repeated Knowlton's diagnosis in his discussion of the species and did not localize the figured material. The bordered pits in one of the three photomicrographs published by Daugherty (1941) are abietinian, not araucarian, and the other two photomicrographs appear not to be *A. arizonicum* secondary xylem as described by Knowlton (1888) or others subsequently (e.g., Scott, 1961; Turkel, 1968; Ash and Savidge, 2004). Thus, it could well be that Daugherty (1941) unwittingly showed that not all of the large logs in PEFO are in fact *A. arizonicum*. Scott (1961) reported that he had examined petrified wood from an unspecified number of localities in the Upper Triassic of the southwestern USA and concluded that all of it belonged to *A. arizonicum.* Turkel (1968) studied the anatomy of several specimens of petrified wood from PEFO for his PhD degree, but he never published his findings. In recent years, the anatomy of *A. arizonicum*-like wood found in PEFO was described in connection with other studies (Ash and Creber, 1992, 2000; Ash and Savidge, 2004).

Within this background, the fossil described here as *Arboramosa semicircumtrachea* n. gen. et n. sp. was earlier assumed to be the upper part of a stem of an *Araucarioxylon arizonicum* tree (Ash and Creber 2000). However, that interpretation was made without having examined the anatomy of the wood. Our observations make it clear that *Arboramosa semicircumtrachea* is unrelated to *A. arizonicum*.

LOCALITY AND REPOSITORY INFORMATION

The stem described here is embedded in the lower part of the Sonsela Member of the Chinle Formation in Crystal Forest, one of the four areas in PEFO containing large concentrations of fossil wood and, therefore, designated a "for-

est" (Ash, 1987). The fossil lies in the Jim Camp Wash Beds, the same unit that contains the petrified logs in Crystal Forest (Parker, this volume).

The site where the stem is situated has been assigned locality number PFP 116 in the collection records of Petrified Forest National Park. Qualified investigators may obtain its exact location from the Chief of Resource Management, Petrified Forest National Park The slides and uncut material removed from the stem are stored in the PEFO fossil collection under catalog number PEFO 34160.

METHODS

To investigate the wood anatomy of the fossil, small samples were chiselled from several locations along the stem, and transverse, radial and tangential surfaces were cut and ground to 30 µm thickness for microscopy. The images presented here (Figs. 2.1 – 4.9) are based on transmitted light microscopy, using a stage micrometer (precision ±2µm) for measurements. Digitized images of both the micrometer scale and the fossil were enlarged by printing, enabling distance estimates to the nearest 0.1µm from measurements on the prints.

A piece of the permineralized wood having good anatomical preservation was analyzed for K, U, and Pb contents by electron microprobe (JEOL-733, equipped with Geller automation, 15 kV, probe current 30 nA), using U metal, crocoite and orthoclase as calibration standards. The average K content of the secondary xylem was very low, 0.011 wt.%. Neither U nor Pb was above detection limits (0.04 wt % and 0.03 wt %, respectively).

OBSERVATIONS

Morphological features.–Measurements of the fossil's surface features were made in the field. The exposed surface of the fossil, shown in Figures 1.1and 1.2, reveals a stem *c.* 8 m in length and 55 cm in basal diameter, tapering somewhat to where the top of the tree becomes overlain with bentonite and round-

Table 1–Known megafossils in Petrified Forest National Park, Arizona, having secondary xylem of diameter more than 1 cm. Listed in order of abundance.

Species and Authority	Number of specimens[1]	Diameter (m)	Taxonomic Division	Stratigraphic Horizon[2]	Principal Locations in the park[2]
Araucarioxylon[3] *arizonicum* Knowlton, 1888	>10000	>1	Coniferophyta	Sonsela Mbr	Rainbow, Crystal, and Jasper Forest
Araucarioxylon[3] *arizonicum* Knowlton, 1888	>1000	>1	Coniferophyta	Black Forest Bed, Petrified Forest Mbr	Lithodendron and Dead Washes
Woodworthia arizonica Jeffrey, 1910	>1000	~0.5	Coniferophyta	Black Forest Bed, Petrified Forest Mbr	Lithodendron and Dead Washes
Schilderia adamanica Daugherty, 1934	>1000	~0.5	Coniferophyta	Black Forest Bed, Petrified Forest Mbr	Lithodendron and Dead Washes
Charmogia dijolli Ash, 1985	2	0.01	Cycadophyta	Blue Mesa Member	Tepees Area
Lyssoxylon grigsbyi Daugherty, 1941	1	0.02	Cycadophyta	Blue Mesa Member	Adamana Area
Dadoxylon chaneyi[4] Daugherty, 1941	1	0.02	Coniferophyta	Blue Mesa Member	Tepees Area
Arboramosa semicircumtrachea gen. et sp. nov	1	~0.5	Coniferophyta	Jim Camp Wash beds	Crystal Forest

Notes: [1]Estimates based on the scientific literature and casual field observations. [2] For more complete information on stratigraphic horizons and localities see Parker, this volume. [3]*Araucarioxylon* is an invalid genus (see text). [4]*Dadoxylon* is an invalid genus (see text).

ed pebbles of about 1 cm diameter. Bark is not present, but the outer surface of the secondary xylem is non-eroded and can be assumed to have been in contact with cambium when the tree was alive. The surface wood grain is straight, though slightly sinuous, at both the basal and apical ends of the exposed stem; however, between those positions it spirals upward to the right at an angle of *c.* 8º from the stem axis. The stem base is not buttressed but is fluted, similar to extant trees within the Cupressaceae (e.g., *Juniperus*, *Taxodium*, and *Thuja* spp.). The branch stubs are positioned within axially oriented fusiform-shaped depressions, or concavities, in the surface wood (Figs. 1.2, 1.3). The manner in which the branches join the stem is unlike that of either *Taxodium* or *Thuja* spp. but is quite similar to that found on older stems of some tree-form junipers, such as *J. virginiana* L. (Figs. 1.4, 1.5). Singular branch stubs occupy some stem depressions, but two or more separated by a few centimeters may also occur in one depression, both on the fossil (Fig. 1.2) and in *J. virginiana* (Fig. 1.4). The branch stubs exhibit only a small increase in diameter over the 8 m from top to base of the fossil. The fusiform depressions with their branch stubs are regularly distributed and could be envisaged as describing either an upward-to-the-left or an upward-to-the-right spiral, again a feature of junipers. The spiralled distribution of branches and the small diameters of the branch stubs are evidence that the tree had a dense crown, possibly conical or columnar in its form.

Tracheidoxyl features.–The secondary xylem is well preserved in some parts of the fossil (Figs. 2, 3, 4). Uniformly thick-walled longitudinal tracheids and homogeneous thin-walled uniseriate ray cells are the only two cell types that could be conclusively identified in the secondary xylem, although scattered axial parenchyma may also be present. Thus, at low magnification (Figs. 2.1, 2.2) the xylem could be confused with Paleozoic Cordaiteae woods, e.g., *Cordaioxylon* or *Mesoxylon*. However, when examined in detail it is more complex than that of cordaites with some quite unusual features. In cross sections of the stem, both the inter-tracheid wall contacts and tracheid lumens rarely exhibit any angularity; generally they are circular, elliptical or semi-circular. Tracheids in adjoining radial files for the most part occupy positions of alternate arrangement, rather than being in ranked tiers (Figs. 2.2, 3.1-3.6). Tracheid diameters vary from <10 to >70 μm. The variable diameters, outlines, arrangement and intercellular spacing give the radial files a jumbled appearance (Figs. 2.2, 3.1-3.3).

Micrometric measurements of the secondary xylem elements provided the following data: single-wall thickness of tracheid secondary walls ranges from 6 to 11 μm, with the S_2 layer being the dominant feature, the S_3 layer *c.* 2 μm and the S_1 less, *c.* 1 μm (Figs. 2.8, 3.4-3.6, 4.9). Tracheid tangential diameter at mid-length is *c.* 55 μm, reaching 70 μm in tracheids of circular cross section (Fig. 2.3). The corresponding width in the radial direction reaches 100 μm in tracheids having semi-circular or elliptical cross sections (Figs. 3.4, 3.6); however, it reduces to as little as 15 μm at growth interruptions (Fig. 2.1), and circular tracheid tips can be less than 10 μm in diameter (Fig. 3.5). Tracheids 10 mm in length are common, and still longer ones were noted (Fig. 2.3). Microfibril angle, measured as the angular deviation from the tracheid long axis, is 32-36º in the S_2 (Figs. 4.1, 4.3- 4.5). The angles in the S_1 and S_3 layers are parallel at *c.* 45º in the orientation opposing that of the S_2 (Figs. 4.1, 4.4). The microfibrils do not display major checking but have conspicuous parallel striations except in the thin S_1 layer where some waviness is evident (Figs. 4.1, 4.8).

Axial parenchyma may be present (Figs. 2.1, 2.5), and tracheids having presumed resinous 'septa' may rarely be found (Fig. 4.3). Evidence for scalariform ribbing of the walls was encountered in a single longitudinal xylem element (Fig. 4.2); that ribbing could not be well resolved and may be artifactual or indicative of an infrequent cell type distinct from the trilaminate tracheids. Axial resin canals and spiral-banded tracheids were not found in the secondary xylem.

The rays in the secondary xylem consist of uniseriate thin-walled parenchyma, only. Viewed in cross section, the rays are widely spaced, not uncommonly separated by more than 20 radial files of tracheids, although less wide spacing is also seen (Figs. 2.1, 2.2). In tangential section, the number of rays in contact with both sides of an individual 10-mm-long tracheid is fewer than 10, a low frequency compared to what has been observed for extant conifers having tracheids only a mm long (Bannan and Bayly, 1956; Bannan, 1965). The rays in the fossil are short (80 – 400 μm)**,** from one to fifteen and usually four to eight cells in height (Figs. 2.3, 2.4, 2.6). Viewed in tangential section, the ray cells are either elliptical or have compressed horizontal walls, with axial diameter *c.* 25-30 μm and horizontal width 10-18 μm (Fig. 2.6). Intercellular spaces within rays are not evident, and spaces created by walls of adjoining rounded tracheids commonly are occupied by ray cells (Figs. 2.8, 3.1-3.6). In radial section, the rays comprise homogeneous, thin-walled, tube-like, non-swollen parenchyma cells, usually with ergastic contents (Figs. 2.4, 2.7). Neither ray tracheids nor horizontal resin canals were seen. Where ray cells and axial tracheids contact, the cross-fields in radial

Figure *1. Arboramosa semicircumtrachea* (*1-3*) and *Juniperus virginia* (*4-5*). *1.* The investigated fossil; a long stem flute can be seen to the right of the hammerhead; *2.* Mid-region of the stem shown in Figure 2.1. Single and multiple branch stubs (arrow heads) having both upward-to-left and upward-to-right spiralling placement exit from fusiform cavities; *3.* Near the apical end of the exposed fossil, showing two or more large fusiform cavities in close proximity (arrow); *4.* Base of *Juniperus virginia* stem showing two branch junctions within a fusiform depression (arrows); *5.* In the upper stem of the same *J. virginia*, the young branches develop prior to the appearance of stem concavities. Scale bars: 2, 3=10 cm; 4=5 cm; 5=2 cm. Images in Figures 1-3 show the holotype, PEFO 34160.
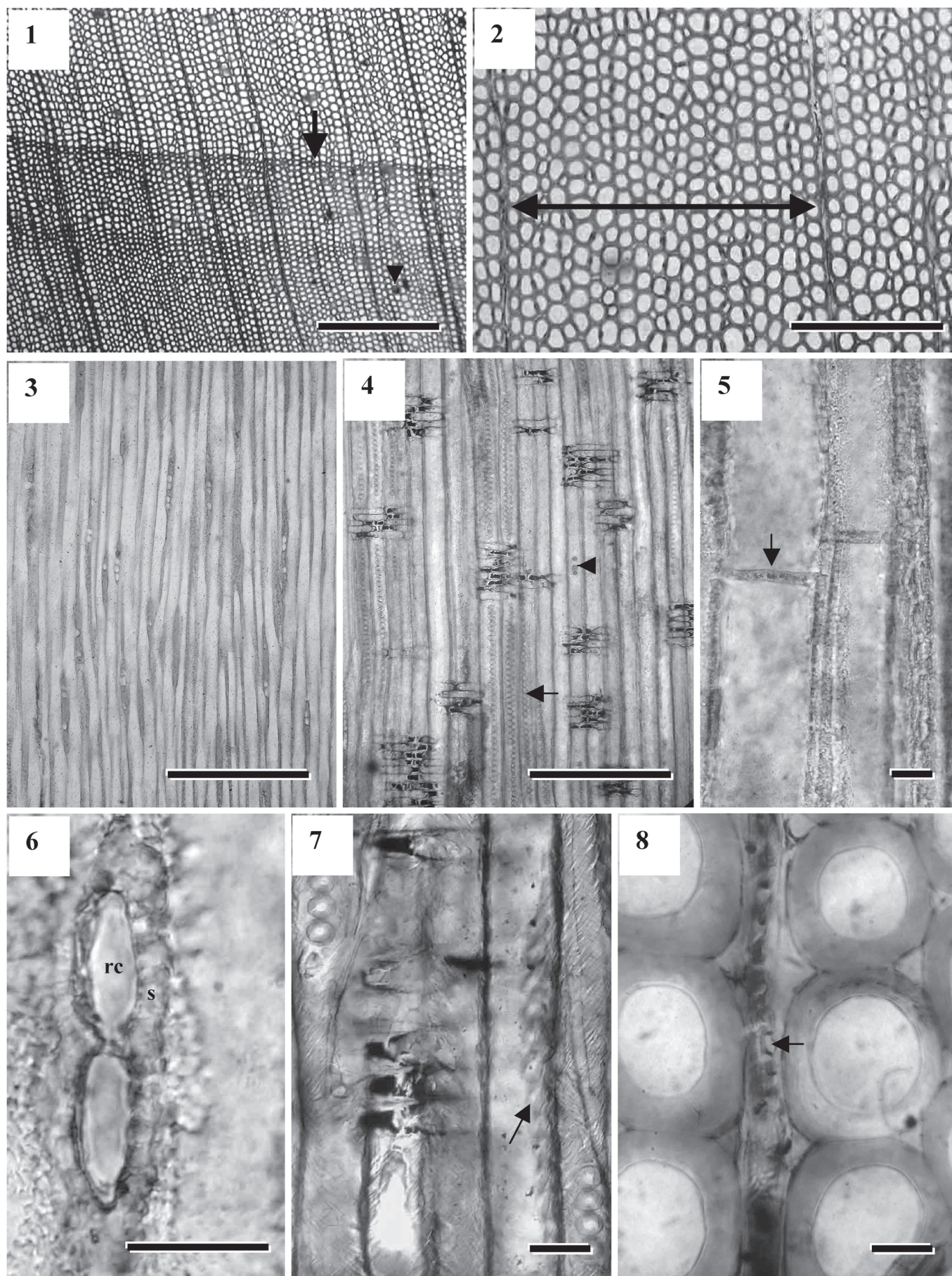
section contain 1 - 6, but usually 4 oculipores equidistantly spaced at *c*. 12 μm apart (Figs. 4.7, 4.8). When four are present, they are positioned at the corners of a square with imaginary connecting lines paralleling the ray cell walls (Fig. 4.8). The long axis of the oculipore aperture is slanted at *c*. 45°. Dimensions of the oculipore border are *c*. 10 μm X 5 μm, with the elliptical aperture > 3 μm wide and extending to 8 μm, never beyond the oculipore border. Similar pitting occurs in the horizontal walls of the ray cells (Fig. 2.8). Pitting of the tangential walls was not seen. By definition, the pits are mostly taxodioid, but cupressoid oculipores having slit-like apertures were also encountered. Borders are not everywhere obvious around the oculipore apertures, and some apertures have an X or V shape, their long axes extending in both the S_1 - S_3 as well as the nearly perpendicular S_2 microfibril directions. Thus, some oopores may also be present, but none were definitively resolved.

Abietinoid bordered pits are abundant in the secondary xylem. Most commonly they occur as long, straight, uniseriate chains of equi-diameter pits, but they are also found in biseriate rank, loosely arranged oppositely or alternately (Figs. 2.4, 2.7, 4.3-4.6). The alignment of pits in the uniseriate chains is parallel to the long axis of the tracheid (Figs. 2.4, 4.3), and a chain of contiguous pits commonly extends for more than a millimeter (Fig. 2.4). The border and aperture of the pits are rounded, usually circular, rarely somewhat flattened horizontally (Fig. 4.3). When in uniseriate rank, the axial distance between bordered pits varies from 3 μm to contacting one another. Where the pits are biseriate and arranged alternately, spaces may or may not separate their margins, so that they can appear to be either abietinoid or araucaroid (Fig. 4.6). Rims of Sanio (crassulae) were not seen.

The horizontal, or circumferential, placement of bordered pits in the walls of tracheids evidently can be at any position where two tracheids are in contact (Figs. 3.1, 3.3). Regardless of where placed circumferentially, bordered pits have the same diameter (16-18 μm) within a narrow range. The bordered-pit aperture (4-5 μm diameter) is generally circular, and a torus is not present. Because of the thickness of the secondary walls, the pit opening tends to be a short cylindrical tunnel extending between the bordered-pit chamber and the lumen (Fig. 3.4). Slit-shaped apertures were infrequently observed and may be artifactual, caused by cell-wall checking. The nature of the bordered pits, manifesting rigid intrinsic

regulation of diameter and vertical alignment but sporadic spacing and placement around the circumference, is unusual.

The rounded tracheids and intercellular spaces seen in cross sections of the fossil recall compression wood (Timell, 1983), as do the relatively steep microfibril angles in the secondary-wall lamellae as seen in longitudinal sections (Figs. 4.1, 4.3-4.5). On the other hand, secondary walls lacking the S_3 layer are characteristic of compression-wood tracheids, and the fossil's secondary walls exhibit tri-laminate S_1, S_2, S_3 layers (Figs. 2.8, 4.9). The spiral checks that are characteristic of the S_2 layer of compression wood are not present in the fossil wood. Moreover, bordered pits are infrequent, even entirely absent, in compression-wood tracheids (Trendelenburg, 1932), whereas the fossil's circular tracheids have abundant bordered pits on all wall surfaces (Figs. 2.4, 2.7, 4.3). When bordered pits do occur in compression wood, the apertures appear to be crossed by diagonal slits that extend beyond the pit annulus and parallel the S_2 microfibrillar orientation within the two adjoining secondary walls (Timell, 1986). In contrast, the apertures in the fossil are circular and do not extend beyond the pit annulus. True compression-wood tracheids tend to be short (Timell, 1986), but the tracheids in the investigated fossil are exceptionally elongated, 10 mm and more in length.

Abrupt, mildly to sharply defined growth interruptions are seen in cross sections of the xylem (Fig. 2.1). The existence of these was determined by measurement to be due to synchronously reduced radial expansion of adjoining cambial derivatives, rather than to an increase in the thickness of the secondary walls, which tend to be uniformly thick throughout the xylem (Fig. 2.1). It cannot be assumed that the rings indicate occurrence of annual cycles of growth and dormancy, as a momentary reduction in radial expansion of cambial derivatives can occur in active cambium in response to a transient limiting supply of an environmental factor, such as water or warmth (Savidge, 1993).

Sections of well-preserved pith were not obtained, but on the basis of both microscopic and macroscopic observation, the pith was of small diameter.

SYSTEMATIC PALEONTOLOGY

Family uncertain
Genus ARBORAMOSA new genus

Figure 2. *Arboramosa semicircumtrachea*. *1*. Cross section showing a growth interruption (arrowed) and evidence for another, less obvious one below. The arrowhead indicates what may be an infrequent resiniferous tracheid or axial parenchyma. Thin section PEFO 34160A1; *2*. Cross section; the arrowed line spans 20+ radial files of tracheids between two rays. Thin section PEFO 34160A1; *3*. Tangential section showing the short, distantly spaced rays. Thin section PEFO 34160C1; *4*. Radial section showing ray heights and the general presence of ergastic material in the ray parenchyma. A long chain of uniseriate pits is indicated by the arrow and an isolated trio by the arrowhead. Thin section PEFO 34160B1; *5*. Tangential section of two septa (one arrowed) indicative of axial parenchyma. Thin section PEFO 34160C1; *6*. Tangential section showing elliptical ray cells (rc) and adjoining secondary wall (s) of a tracheids. Thin section PEFO 34160C1; *7*. Radial section showing bordered pits on diagonally oriented (arrowed) as well as radial walls. Thin section PEFO 34160B1; *8*. Cross section showing taxodioid/cupressoid oculipores (one arrowed) in the horizontal walls of ray cells. Thin section PEFO 34160A1. Scale bars: 1=1 mm; 2-4=0.5 mm; 5=20 μm; 6=25 μm; 7=50 μm; 8=20 μm. All sections made from the holotype PEFO 34160.
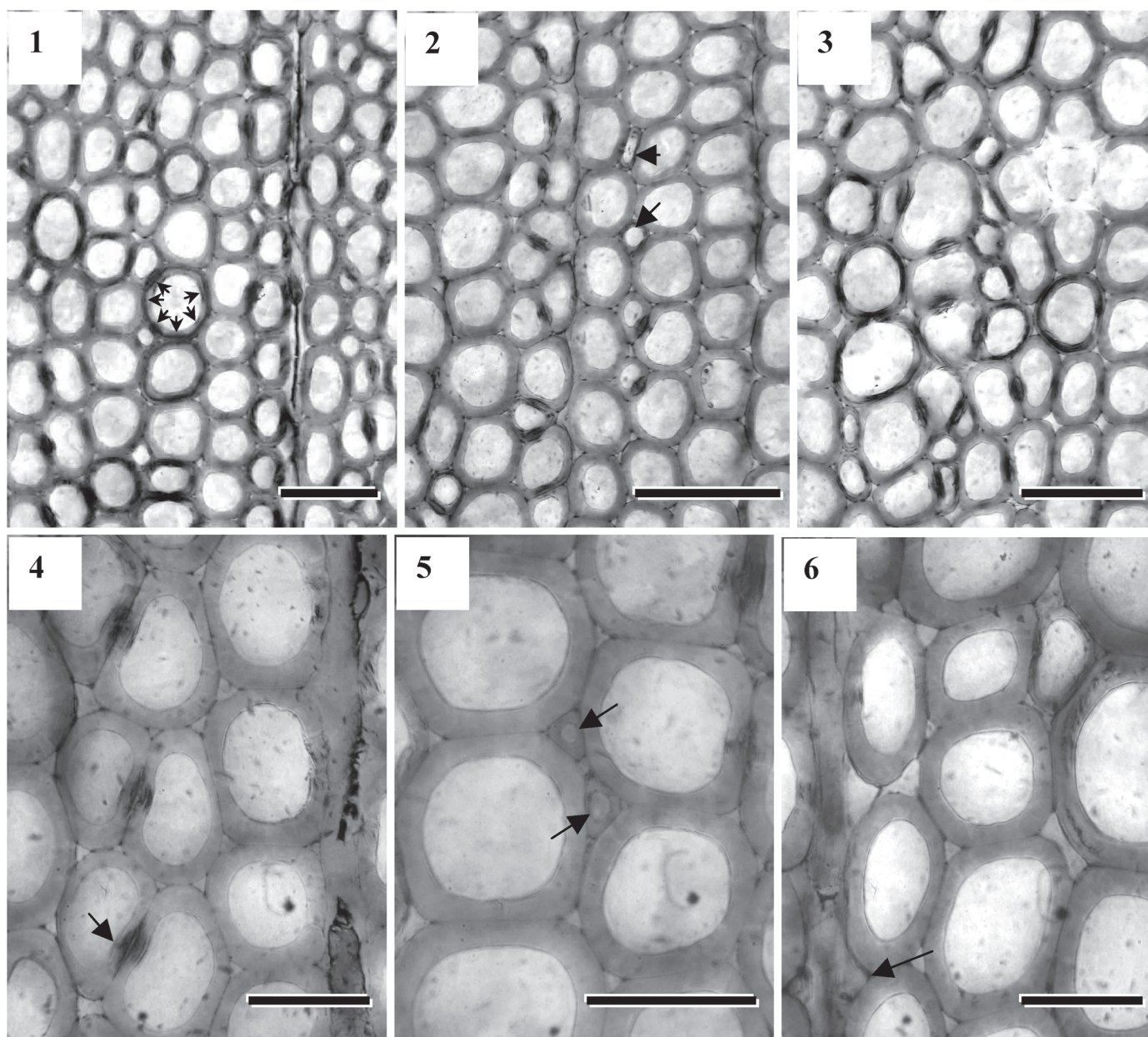
Figure 3. *Arboramosa semicircumtrachea*. Cross sections of the fossil's secondary xylem. *1*. Note the variable diameter but generally thick-walled tracheids. The six arrowheads indicate six bordered-pit pairs at positions around the circumference where the circular tracheid contacts other tracheids; *2*. Tapered tracheid ends (arrowed) can be seen intruding between the radial files. Note the irregular placement of the bordered-pit pairs, conspicuous in the diagonal walls; *3*. Tracheid radial files are poorly organized due to tracheid circularity, variable diameter and intrusive growth; *4*. Semi-rounded tracheids having bordered-pit pairs (one is arrowed) in their straight, diagonally oriented walls; *5*. Small-diameter thick-walled tracheid tips (arrows) occupy locations that otherwise would be intercellular spaces; *6*. Tracheids, particularly where they adjoin rays, exhibit radially stretched, rounded outlines in cross section. The thin primary walls of ray parenchyma cells evidently grow into intercellular spaces between the circular tracheids (arrow). Scale bars: 1-3=100 µm; 4-6=50 µm. All images were made from the holotype, thin section PEFO 34160A1.

Type species.–*Arboramosa semicircumtrachea* sp. nov. by monotypy.

Diagnosis.–Secondary xylem surface with fusiform-shaped cavities parallel to main stem axis in regular spiralled arrangement; lateral branch stubs egress from fusiform-shaped cavities. Secondary xylem tracheids round to semi-round in transverse section, having bordered pits on all wall surfaces, mixed but mostly abietinian pitting, axial parenchyma present but scarce; xylem pycnoxylic, composed of thin-walled homogeneous uniseriate ray cells, oculipore cross-field pittting; other parenchyma wanting.

Description.–The wood surface of the main stem has a coarsely braided appearance because of its axially oriented fusiform-shaped concavities and the slightly enhanced secondary growth of the stem around the boundaries of those depressions (Figs. 1.1-1.3). The placement of the fusiform concavities is well spaced, precisely regular and could be interpreted as spiralling, either upward-to-the-left or upward-to-

the-right, at an angle of *c*. 45º (Fig. 1.2). Branches, or stubs of former branches, connect with the stem within the fusiform depressions. Singular branch stubs occur in some, but two or more may be in close association within the same concavity, one a few cm above the other (Fig. 1.2). The branch stubs generally are of small diameter, being a few centimeters or less on a stem 50 cm in diameter and exhibiting only a small decrease in diameter with increasing stem height, an indication that the branch bases possessed limited capacity for secondary growth when living. Some of the branch bases probably had persisted on the stem of the living tree as dead branch wood. The base of the fossil is grooved, or fluted, in the axial direction over distances exceeding a meter.

Etymology.–The Latin *arbor* (tree) and *ramosa* (branchy) were combined to denote the branchiness of the tree.

Occurrence.–PEFO locality number PFP 116 in the Jim Camp Wash Beds in the Sonsela Member of the Chinle Formation (minimum age of 210 Ma, Riggs et al., 2003).

Discussion.–Branches or branch stubs provide a morphological record of the earlier activity of shoot apical meristems from which the branches originate (Fahn, 1977), as well as that of the vascular cambium, whereas the phenotype of a tracheidoxyl fragment or a decorticated stem or log surface with little or no branching contains only a record of the activity of the lateral meristem (Bannan and Bayly, 1956; Bannan, 1965; Fahn, 1973). The stem morphology is that of extant Cupressaceae, and *Arboramosa* n. gen. fails to satisfy the conditions needed for it to be placed in any recognized Mesozoic conifer, ginkgoalean or cordaitean family on the basis of its tracheidoxyl anatomy. The institution of a new family to include *Arboramosa* n. gen. stem morphology and its novel tracheidoxyl characteristics evidently is in order, but before proposing one, we foresee the need for additional research to characterize the anatomy of pith and primary xylem.

Crowns with densely and spirally arranged branches are common in Cupressaceae, but the manner in which the branches of *Arboramosa* n. gen. connect to the stem within fusiform-shaped concavities (Figs. 1A-1C) is not a general Cupressaceae trait. The form and branch junctions displayed by *Arboramosa* n. gen. are, however, characteristics of some *Juniperus* trees (Figs. 1D-1E). Although *Arboramosa* n. gen. appears to be a juniper-like conifer, the megafossil contains stem-surface features not previously reported in fossilized trees of Triassic age or earlier.

Walchia, Ernestiodendron and *Ortiseia* spp. of the family Walchiaceae (Order Voltziales, Cordaiteae) found in Upper Carboniferous and Permian localities are believed ancestral to living conifers, but unlike the regular spiralled branching found on *Arboramosa* n. gen., those trees had whorled branching patterns (Florin, 1944). The coarsely braided secondary xylem surface and the regular, spiralled distribution of branches on *Arboramosa* n. gen. distinguish it readily from other petrified logs in PEFO. Larger diameter specimens of Upper Triassic *Schilderia adamanica* from the Chinle Formation do have in common with *Arboramosa* n. gen. a fluted stem phenotype (Daugherty, 1941; Creber and Ash, 2004). However, *S. adamanica* does not have branch junctions within fusiform depressions. In addition, *Arboramosa* n. gen. secondary xylem is pycnoxylic whereas that of *S. adamanica* is conspicuously manoxylic. Tracheidoxyl details of *Arboramosa* n. gen. are given emphasis below under the species designation, but some consideration of the history of taxonomical classification is needed here because the names of many genera are based on tracheidoxyl features alone.

Lindley and Hutton (1832) initiated the genus *Pinites* in describing three woods having multiseriate rays, and Witham (1833) used the identical name to describe woods having alternate, polygonal bordered pits (araucarian pitting) on tracheid radial walls. Witham (1833) instituted the genus *Pitus* and distinguished it from *Pinites* on the basis that *Pitus* usually has circular (abietinian) bordered pits in biseriate or triseriate rank, with spaces between the bordered pits, whereas *Pinites* has contiguous hexagonal bordered pits in biseriate or higher rank, like modern species of *Araucaria* and *Agathis*. Although containing many anatomical features of extant conifer woods, both *Pitus* and *Pinites* contain multiseriate as well as uniseriate rays, *Pitus* 4-15 cells in width and *Pinites* 2-5 cells in width (Witham 1833). Technically, therefore, both *Pitus* and *Pinites* are manoxylic woods unlike araucarian or abietinian conifers, but in considering the wood described as *Pinites* by Witham (1833), Göppert (1850) nevertheless decided that it should be renamed *Araucarites*, and he retained the genus *Pinites* to refer to woods similar to those within extant Pinaceae (those which Witham 1833 had described as *Pitus*). Göppert's use of *Araucarites* was in error because Endlicher (1847) had earlier stated that *Araucarites* should not be used to refer to wood of *Araucaria*-like fossils and had instituted *Dadoxylon* to refer to such tracheidoxyls. Moreover, Hartig (1848) had already named the genus *Agathoxylon* (also known as *Dammaroxylon*) on the basis of the same, or very similar, tracheidoxyl features recognized by Göppert (1850) for *Araucarites*. Probably as a result of this nomenclatural confusion, Kraus (1870) later initiated *Araucaroxylon* (sic) from *Araucarites*. Early Devonian specimens that had been designated *Dadoxylon* by Dawson (1871) were subsequently considered to be Paleozoic ancestors, if not equivalents, to *Araucaroxylon* (sic), as were Cordaitae of the Carboniferous and Permian periods (Solms-Laubach 1891). Consequently, both *Dadoxylon* and *Araucarioxylon* are taxonomically invalid (Seward 1917; Philippe, 1993; Bamford and Philippe, 2001) and many Permian and Triassic specimens with those names have been reassigned to the genus *Agathoxylon* named by Hartig (1848).
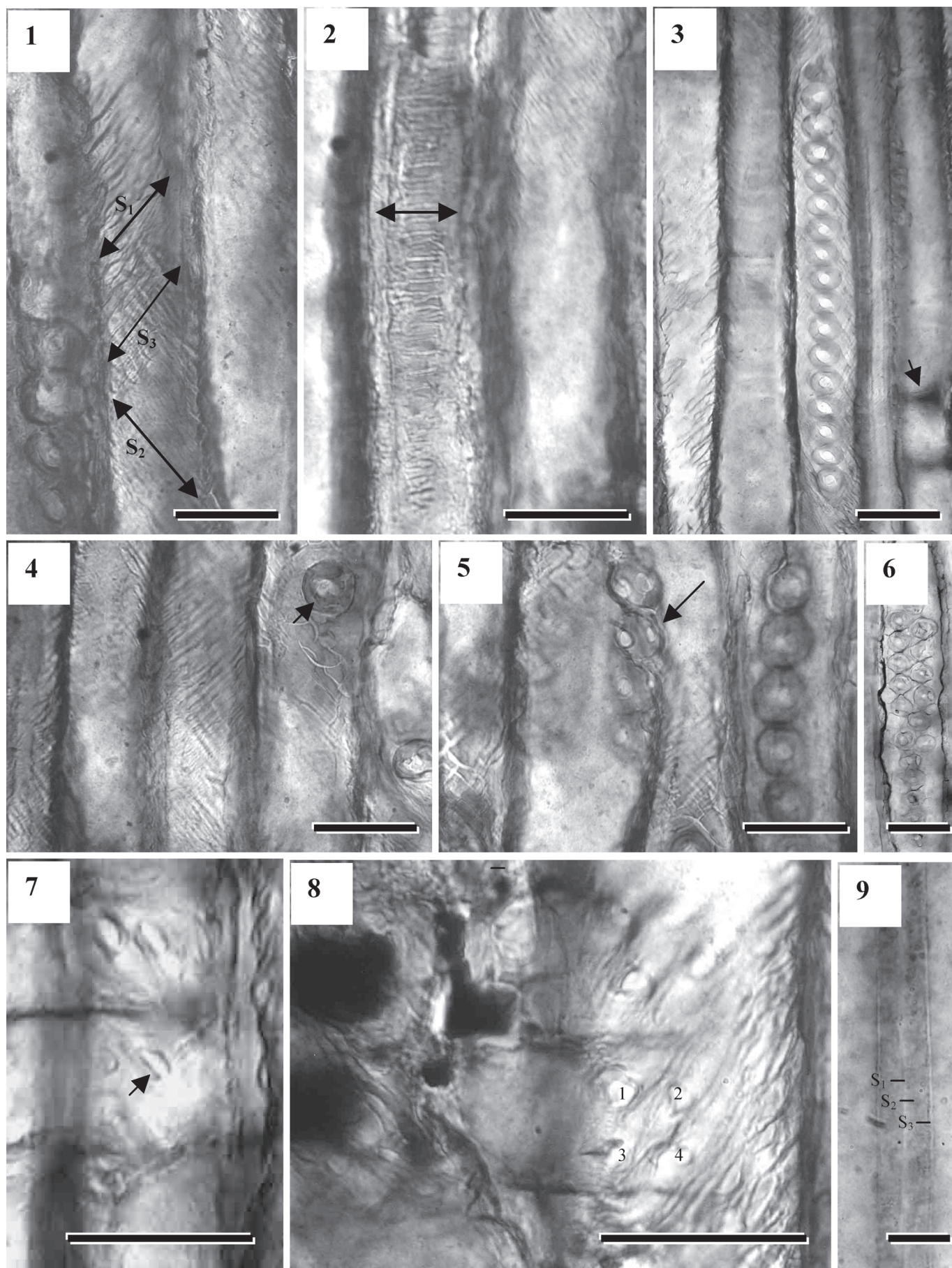
In addition to *Araucarites* and *Pinites*, Göppert (1850) initiated *Cupressinoxylon* and *Taxites* to refer to two additional genera of fossil woods that are anatomically different from *Araucarites* and *Pinites*. *Cupressinoxylon* woods were to resemble those of extant Cupressaceae and Podocarpaceae, *Taxites* woods the Taxaceae. Kraus (1870) subsequently initiated *Cedroxylon* to include woods identical with *Cupressinoxylon* except for lacking resiniferous elements otherwise seen as longitudinal (i.e., axial) parenchyma cells, and various questionable relatives of *Cedroxylon* subsequently were named (Philippe, 2002).

Arboramosa n. gen. secondary xylem superficially satisfies assignment to the genus *Cedroxylon* (Kraus, 1870); however, it actually is quite different from other *Cedroxylon* woods that have been figured (e.g., Stopes, 1915; Morgans, 1999) because of its disorganized radial files, rounded tracheids and circumferentially distributed bordered pits. Moreover, according to Kraus (1870) *Cedroxylon* wood is similar to *Cupressinoxylon* but, as expressed by Bamford and Phillipe (2001), the situation with *Cupressinoxylon* remains a "terrible imbroglio." *Cupressinoxylon* was to be distinguished from the other three types instituted by Göppert (1850) on the basis of having bordered pits separate, in one row, or, if in more than one, the pits of different rows opposite one another, longitudinal parenchyma containing resin present; resin canals absent (Göppert, 1850). When these criteria were applied in practice, it was soon recognized that *Cupressinoxylon* was an artificial supergenus crossing taxonomic boundaries, not only comprising the Cupressaceae but also species in *Abies* and even *Ginkgo biloba* (Barber, 1898). Moreover, the criteria for inclusion in *Cupressinoxylon* failed to adequately embrace some members of the Cupressaceae (Vaudois and Privé, 1971; Bamford and Phillipe, 2001). In view of the continuing revision attending *Cedroxylon* and *Cupressinoxylon*, and taking into consideration the entirely distinctive features of the investigated tracheidoxyl, both of those genera were avoided in the present assignment.

The tracheidoxyl features of *Arboramosa* n. gen. satisfy the unusual dual requirement of taxodioid cross-field pitting and abietinian tracheid radial wall pitting that justified *Protaxodioxylon* as a new tracheidoxyl genus (Bamford and Philippe, 2001). In this respect, *Arboramosa* n. gen. again appears to have affinity with Cupressaceae. However, longitudinal parenchyma cells are common and diagnostic of Cupressaceae including junipers (Vaudois and Privé, 1971), and that cell type is scarce in *Arboramosa* n. gen. Junipers sometimes exhibit rounded normal-wood tracheids in cross section (Phillips, 1948; McGinnes and Phelps, 1972), but they do not have semi-circular tracheids with one diagonally oriented wall, nor do they produce bordered pits equally on all wall surfaces. These homology shortcomings aside, the major difficulty with assignment of the investigated fossil to *Juniperoxylon* (Houlbert, 1910: *J. turonense* Houlbert) is that fossils of definitive juniper-like wood earlier than the Cenozoic (Tertiary, Middle Eocene) are unknown, and investigations into reproductive structures have raised doubt about the idea that any member of Cupressaceae existed in the Mesozoic or earlier (Watson, 1988). It would be difficult to justify a 160 Ma gap in the fossil record between *Arboramosa* n. gen. as a *Juniperus* predecessor and the existing Cenozoic specimens of *Juniperoxylon*, but more research is clearly needed to determine if the gap can be narrowed. Upper Jurassic *Protocupressinoxylon purbeckensis* was found to have shoots and leaves similar to modern *Thuja plicata* (Cupressaceae), and its wood displays several anatomical features similar to those in wood of *Arboramosa* n. gen., including a scarcity of longitudinal parenchyma and the presence of rounded tracheids. However, semi-circular tracheids with bordered pits on diagonal walls were not reported, and biseriate pitting was described as always opposite (Francis, 1983), making *Protocupressinoxylon purbeckensis* distinct from *Arboramosa* n. gen. Jurassic *Protaxodioxylon* (Bamford and Philippe, 2001) is different from *Arboramosa* n. gen. in having conspicuous longitudinal parenchyma and in having its taxodioid cross-field pit apertures horizontally oriented (see, for example, Morgans, 1999). Similar concerns pertain to Upper Triassic *Taxodioxylon* and *Cupressinoxylon* (Schweitzer,1963; Vaudois and Privé, 1971; Stewart, 1983). In cross sections, rounded tracheids with bordered pits on all wall surfaces are prevalent distinguishing features in *Arboramosa* n. gen**.**, and those features evidently are unknown (or have been overlooked) in *Protaxodioxylon*, *Taxodioxylon* and *Cupressinoxylon*. Petrified tree trunks referred to as *Protojuniperoxylon ischigualastianus* in Upper Triassic (Carnian) deposits of the Ischigualasto Formation in northwestern Argentina are presumed to be unlike *Arboramosa* n. gen., as they were described as those of the Araucariaceae (Romer, 1962). The stem surface features

Figure *4*. *Arboramosa semicircumtrachea. 1*. Microfibril orientations of the somewhat wavy S_1, thick S_2 and adjoining S_3 layers are indicated by the arrowed lines; *2* Horizontally oriented microfibrils are indicated by the arrowed line in a rare xylem cell type (plausibly, an axial parenchyma cell); *3*. A chain of uniseriate circular (abietinoid) bordered pits with circular apertures in a radial wall; a possible resin plug in a tracheid is arrowed; *4*. Singular, isolated abietinoid bordered pits (one arrowed) occur in radial walls; *5*. A bordered pit pair between diagonal walls is arrowed; their diameters are similar to those in radial walls, as evident in the short abietinoid chain above the scale bar; *6*. Tracheid with biseriate pitting; although some pits are araucaroid-like, most are circular and not in contact with one another; *7*. Radial section showing oculipores (taxodioid/cupressoid) in cross fields; a pit border of one is arrowed; *8*. Numbered oculipores in a cross field; four are commonly present and positioned at the points of a square; *9*. Radial section of secondary walls of two adjoining tracheids, showing the very thin S_1, thick S_2 and thin S_3 layers. Scale bars: 1-8=50 µm; 9=20 µm. All images were made from the holotype, thin section PEFO 34160B1.

and branching pattern of *Protaxodioxylon, Taxodioxylon*, *Cupressinoxylon* and *P. ischigualastianus* evidently remain to be described.

ARBORAMOSA SEMICIRCUMTRACHEA new species
Figures 1.1-1.3, 2-4

Diagnosis.– Pycnoxylic secondary xylem. In transverse section, tracheids in disorganized radial files, circular or elliptical with rounded lumens and intercellular spaces; secondary walls thick with three layers, S_2 thickest, one double wall of adjoining tracheids frequently oriented diagonally rather than radially; equi-diameter bordered pits on all wall surfaces; small diameter tracheid tips intrude into intercellular spaces; axial parenchyma present but infrequent; no longitudinal resin canals; rays uniseriate, infrequent, sometimes separated by 20+ radial files of tracheids; ray cells thin-walled, cylindrical, homogeneous; radial walls extend sideways into intercellular spaces created by adjoining rounded tracheids. In longitudinal sections, circular (abietinoid), equi-diameter bordered pits occur in radial, tangential and diagonal walls of tracheids, torus not evident; uniseriate bordered-pit chains usually long but also occurring as short runs or individual bordered pits; chains linearly aligned parallel to tracheid long axis but curving on diagonal walls; biseriate bordered pits present but uncommon, abietinoid or araucoid where biseriate; transverse septations indicative of axial parenchyma or trabeculae. In radial section, ray cells thin-walled, homogeneous, containing ergastic substances; taxodioid or less commonly cupressoid cross-field pitting with 1-6 usually 4 oculipores per cross field, pit apertures inclined at *c.* 45 degrees. In tangential section, tracheids commonly 10 mm long, non-septated, lacking spiral bands; rays strictly uniseriate, short (80–400 µm), usually 4–8 cells; fewer than 10 rays in contact with both sides of 10 mm-long tracheids; ray cells upright, either elliptical or with compressed horizontal walls; no horizontal resin canals.

Description.– *A. semicircumtrachea* has the characteristic stem morphology of the genus *Arboramosa* (described above), and the species is distinguished by its novel tracheidoxyl anatomy.

Etymology.– The Latin terms *semi* (half), *circum* (around)**,** *trachea* (tracheid) were chosen to describe the semi-circular tracheids seen in cross sections.

Occurrence.– Single holotype specimen (see *Arboramosa* n. gen. above).

Discussion.– Rounded tracheids having three secondary wall lamellae and intercellular spaces like those of *A. semicircumtrachea* can also be found, but not so generally distributed, in normal stem wood of *Juniperus* and *Ginkgo* spp. (Phillips, 1948; McGinnes and Phelps, 1972; Timell, 1983, 1986). Rounded elements and associated intercellular spaces occupy 10 % or less of the surface area in those extant woods,

whereas in *A. semicircumtrachea* it is rare to find anything but rounded tracheids with associated intercellular spaces. Abietinian bordered pitting is largely restricted to the radial walls of *Juniperus* and *Ginkgo* tracheids, whereas abietinian bordered pits are present on all wall surfaces of the rounded tracheids in *A.. semicircumtrachea.* To our knowledge this anatomical phenotype has no precedent. Cross-field pitting in *A. semicircumtrachea* is predominantly taxodioid, less commonly cupressoid (Figs. 2.8, 4.7, 4.8). The distinction between taxodioid and cupressoid pits is based on the width of the aperture *vis-à-vis* the pit border, and it is not uncommon for the aperture width to vary such that both types co-occur. Cupressoid pitting is reportedly diagnostic of *Juniperus* spp. (Panshin and de Zeeuw, 1970), but taxodioid pitting can readily be found also (R. A. Savidge, personal data). *Ginkgo biloba* L. has a mixture of taxodioid - cupressoid pitting (R. A. Savidge, personal data). In terms of numbers of pits and their positioning in the cross field, *G. biloba* is similar to *A. semicircumtrachea* whereas junipers generally have only one or two pits per cross field.

Disorganized radial files of secondary xylem are diagnostic of Ginkgoales (Scott et al., 1962), and in this respect the tracheidoxyl phenotype of *A. semicircumtrachea* more closely resembles ginkgo than juniper. In cross sections of *Ginkgo biloba*, although angular tracheids are the more common, circular or elliptical tracheids having the occasional diagonal wall can sometimes be found (R. A. Savidge, personal data). The conspicuously intruded tips found in *A. semicircumtrachea* indicate abrupt, vigorous elongation of fusiform cambial derivatives. Evidence for abrupt intrusive tip growth is difficult to detect in extant conifers, and the tips evidently extend only marginally as stem diameter growth proceeds (Bannan, 1965; Savidge and Farrar, 1984). Intruded tracheid tips like those found in *A. semicircumtrachea* do occur in cross sections of *G. biloba* secondary xylem (R. A. Savidge, personal data). *A. semicircumtrachea* and *G. biloba* both have uniseriate, short rays. However, *A. semicircumtrachea* ray cells are not bulging or barrel-shaped, but they are conspicuously so in *G. biloba*.

The bordered pits of *A. semicircumtrachea* are equidiameter and for the most part positioned in the tracheid walls as very well ordered, long linear chains parallel to the tracheid axis. Although the pits have spaces between them, crassulae are lacking. These features distinguish *A. semicircumtrachea* from *G. biloba* and *Juniperus* spp. Bordered pits in *G. biloba* tend to be of variable diameter and, when uniseriate, placed in weakly ordered arrangement on the radial walls (R. A. Savidge, personal data). When ginkgo bordered pits on radial walls of tracheids are biseriate, as they frequently are, they are almost invariably placed opposite one another, with crassulae obvious, and crassulae are also present in junipers (R. A. Savidge, personal data). In *A.*

Table *2*. Anatomical features of *Arboramosa semicircumtrachea* compared with those of previously described species in Petrified Forest National Park.

Secondary xylem feature	*Arboramosa semicircumtrachea* [1]	*Araucarioxylon arizonicum* [2,4]	*Woodworthia arizonica* [3,4]	*Schilderia adamanica* [3,4]	*Dadoxylon chaneyi* [3]	*Lissoxylon grigsbyi* [3]
Tracheid radial files	disorganized	well organized	well organized	organized	organized	well organized
Secondary-wall thickness	uniformly thick	variable	variable	uniformly thick	variable	variable
Tracheid (X section)	round/semi-round	angular or round	angular	angular or round	angular	angular
Lumen (X section)	rounded	angular or round	angular	angular or round	angular or round	round
Intercellular spaces	very common	rare to common	rare	occasional	occasional	no
Trabeculae	no	no	no	yes (hyphae?)	yes	no
Spiral-banded tracheids	no	no	no	no	no	yes
Bordered-pit outline	circular/angular	angular/circular	angular/circular	angular/circular	angular/circular	angular
Crassulae	not evident	flattened contacts	flattened contacts	flattened contacts	yes	not evident
Bordered-pit wall placement	on all wall surfaces	radial, sparse on tangental	radial, sparse on tangental	both radial and tangental	both radial and tangental	radial, only
Bordered-pit diameter variation	constant (16-18 μm) on all walls	radial: 20μm tangential: 3μm	radial: 18μm tangential: 9μm	radial: 14x18μm tangential: variable	radial: 9-18μm tangential: c. 6μm	radial: 6-10μm
Bordered-pit chains[5]	uniseriate, long; biseriate, short	uni- and biseriate, short	uniseriate, long; biseriate, short	uni- and biseriate, short	uni- and biseriate, short	uni-, bi-, and triseriate, short
Chain axial organization	linear	scattered	mostly linear	weakly linear	mostly linear	weakly linear
Rays	uniseriate	uni- and biseriate	uniseriate, also short-shoot traces	uni- to multiseriate	uni- to biseriate	uni- to multiseriate
Ray spacing (X section)	6-20 radial files	1-8 radial files	2-10 radial files	1-10 radial files	2-10 radial files	1-6 radial files
Ray height (cell number)	1-15	1-40	1-10	1-12	1-5	4-50
Uniseriate ray width (μm)	10-18	12-30	18	10	18	11
Ray-cell tangential shape	elliptical	circular, flattened	oval, oblong	variable	elliptical	variable
Ray-cell wall thickness	thin	thin	medium	thin	thin to thick	thin to thick
Cross-field pit type	taxodioid/cupressoid	oopores?[6]	taxodioid	taxodioid and oopores	taxodioid	piceoid?[6]
Number of pits/field	1-6 (4 commonly)	elusive[6]	2-8	2-6	1-6	2-5
Cross-field pit orientation	45°	elusive[6]	45°	variable	45°	unstated[6]
Resiniferous tracheids	no, or sparse	yes, common	yes, numerous	no	sparse	no
Axial parenchyma	probably[6]	no	no	yes	no	sparse
Tyloses	no	no	no	no	yes	yes
Horizontal resin canals	no	no	no, short-shoot traces numerous	no	no	yes

Sources and footnotes:
[1] As described herein
[2] Knowlton 1888, Jeffrey 1913
[3] Daugherty 1941
[4] R. A. Savidge, unpublished data
[5] (long, >1 mm; short, < 0.1mm)
[6] Remains to be resolved

semicircumtrachea, where biseriate bordered-pit placement occurs, the pits show no bias toward being opposite one another. They may be alternate and spaced, alternate and adpressed (araucarian-like), or opposite, but regardless of the arrangement, crassulae are not present. Tangential wall pitting of ginkgo and juniper tracheids generally occurs only in the latewood, and when present the pits are of much smaller diameter than the radial wall pits (R. A. Savidge, personal data). In contrast, pit placement in *A. semicircumtrachea* occurs at any location around the tracheid circumference and is everywhere equi-diameter.

Axial, or longitudinal, parenchyma are present to a limited extent in secondary xylem of juniper species and ginkgo (Phillips, 1948; McGinnes and Phelps, 1972; Panshin and de Zeeuw, 1970), and they also appear to be present but rare in *A. semicircumtrachea*. The walls of *A. semicircumtrachea* are generally thick; that is, the xylem lacks the sporadically distributed thin-walled large diameter parenchyma cells commonly found among thicker-walled, smaller diameter tracheids in *G. biloba*. Calcium oxalate crystals, common in the enlarged parenchyma of ginkgo, were not seen in the fossil.

The rounded, multi-pitted tracheids in *A. semicircumtrachea* do not strictly satisfy the definition of compression wood (Timell, 1986). Their prevalence in the wood is nevertheless instructive, providing evidence that the phenomena of cell rounding and concomitant formation of intercellular spaces are probably not factors preventing production of either the S₃ layer or bordered pits during formation of true compression wood in extant conifers. Greguss (1967) considered a Permian specimen of *Araucarioxylon* to have some features of compression wood, and Daugherty (1941) noted that *Dadoxylon chaneyi* contained zones of "rotholz" (German for redwood, synonymous with compression wood), but the only authentic tracheidoxyl compression wood so far observed is from the recent Pleistocene (Morey and Morey, 1969; Timell, 1983, 1986).

Agathoxylon (*Dadoxylon/Araucarioxylon*) genera have been broadly defined to encompass considerable variation (Jeffrey, 1910, 1913; Grambast, 1960; Greguss, 1961, 1967; Lepeckhina, 1972; Mussa, 1982), but even so the latitude is not sufficiently broad to permit inclusion of the qualitative tracheidoxyl features reported here for *Arboramosa semicircumtrachea* n. gen. et n. sp. (Table 2).

GENERAL DISCUSSION

The distinguishing characteristics of tracheidoxyls used by Göppert (1858) to diagnose *Araucarites* and later by Kraus (1870) to diagnose *Araucaroxylon* (*sic*) were 1) bordered pits in one row with contact and mutual compression (i.e., adpression), or alternating in several rows and becoming polygonal from mutual adpression, 2) uniseriate rays, and 3) rims

of Sanio (crassulae) lacking. In other words, the tracheidoxyl was to have araucaroid bordered pits with angular margins similar to those found on the radial walls of tracheids in modern *Araucaria* and *Agathis* spp. and in contrast to the abietinoid pits found in most other conifers. Abietinoid pits in tracheid radial walls are non-adpressed, circularly outlined, and generally are separated by crassulae. Woods exhibiting both araucarian and abietinean bordered pits are of the "mixed" type and are found in the Mesozoic and later (Bamford and Philippe 2001). *A. semicircumtrachea* pitting is mixed but primarily abietinean, except that crassulae are wanting. On this basis, the tree evidently was either transitional from an araucarian to an abietinian conifer or was a genetic anomaly within the largely araucarian realm of PEFO woods. The cell biology/biochemistry of pit formation during xylogenesis evidently involves the biogenesis and placement against developing cell walls of an organelle (Savidge 2000, 2003), but the processes of both bordered-pit and crassula formation remain poorly understood biochemically and genetically. Consequently, it is difficult to rationalize tracheidoxyl development and evolution on the basis of the two kinds of pitting.

The development within *A. semicircumtrachea* of semi-circular tracheids with one wall diagonally oriented, relative to the radial line created by the radial file as seen in cross section, is a novel feature not seen in reports on other tracheidoxyls. As noted above, rounded tracheids with three secondary-wall layers do occasionally occur in normal wood of a few extant conifer species; however, semi-rounded tracheids with one straight diagonally oriented wall occur rarely except in *Ginkgo biloba*. The template for such development evidently arises when one side of a thin-walled, differentiating cambial derivative is compressed (by turgor pressure) against the corresponding walls of two similar cells (one slightly more advanced than the other in its stage of differentiation) within an adjoining radial file (Savidge and Farrar, 1984). The existence of alternately ranked cambial derivatives in adjoining radial files, in conjunction with their different degrees of intercellular bonding, probably provides the fulcrum needed for partially rotating the cells circumferentially as they change from their rectangular outline on the periphery of the cambium to rounded 'tubes' in the zone where they begin to be incorporated into the xylem. The turgor pressure within the cells was obviously sufficient to support attainment of the rounded shape and must also have been a factor contributing to one side becoming flattened to produce the diagonally oriented double-wall contact. Intrusive elongation of tips of primary-walled fusiform cambial derivatives probably occurred during or soon after they had rounded and concomitantly generated intercellular spaces that served as elongation corridors (Hejnowicz, 1961; Savidge and Farrar, 1984).

If enlarged parenchyma with calcium oxalate druses were present in the secondary xylem, if the ray cells were bulging rather than cylindrical, and if the bordered pits were not equi-diameter and when biseriate were opposed to one another with the pairs separated by crassulae, the tracheidoxyl of *A. semicircumtrachea* would likely be aligned with the Ginkgoales. On the basis of leaf impressions, Ginkgoales is believed to date to the Permian, so perhaps it is not far-fetched to imagine *A. semicircumtrachea* as a gingkoalean derivative on its way toward becoming a conifer.

On the other hand, if longitudinal parenchyma were more conspicuous in *A. semicircumtrachea*, and if one were prepared to overlook the general occurrence of rounded tracheids and the circumferential distribution of bordered pits, a case could be made for the tree being in the Cupressaceae and, considering its stem morphological features, possibly even being an ancestor of *Juniperus* spp. The scarcity of longitudinal parenchyma in *A. semicircumtrachea* may not be a major obstacle. Experimentally, fusiform cambial derivatives differentiate as axial parenchyma rather than as tracheids when auxin is in short supply (Savidge and Wareing, 1981; Savidge 1983, 1988), and it is plausible that a minor genetic change in auxin production by leaves or apical meristems is the physiological basis underlying the ability of Cupresseaceae to produce longitudinal parenchyma.

The presence or absence of growth rings or even of partial rings in secondary xylem has frequently been discussed in relation to taxonomic discrimination; however, it should also be considered that growth rings in *A. semicircumtrachea* may be merely adaptive features indicative of the physiological plasticity inherent to woody plants and expressed as needed when climate was non-conducive to ongoing cambial growth (Savidge, 1993). The seasonally mild growing conditions of the PEFO site in the Late Triassic are manifested by the absence of annual growth interruptions in the wood of *A. arizonicum* (Ash and Creber, 1992; Ash and Savidge, 2004).

On the basis of fossil leaves and petrified wood found within PEFO, vascular plant diversity during the Late Triassic included cycadeoids, ginkgoaleans, sphenopsids, ferns, caytonialean pteridosperms and trees possibly related to extant Gnetales (Daugherty, 1941; Krassilov and Ash, 1988; Ash, 1989, 1992, 2001a, 2001b; Creber and Ash, 2004; Pigg et al., 1993). This agrees well with succession inferred by investigations into phytochrome gene sequences from which the divergence period for Gnetatae, Ginkgoatae, and Cycadatae was estimated to be in the Permian and that of the Pinatae in the Triassic (Schmidt and Schneider-Poetsch, 2002). *A. semicircumtrachea*. was an unusual tree and, in relation to its unique secondary xylem, it was a genetic anomaly. *A. semicircumtrachea* appears to be an example of abrupt speciation, possibly arising in response to either a single mutation event or by polyploidisation (Dynesius and Jansson, 2000). Its pronounced branchiness and unusual wood anatomical traits are evidence for pleiotropic control of particular aspects of primary and secondary growth that, until now, have evaded physiological understanding (Savidge, 2001). If the tree's branchiness is considered as evidence for enhanced photosynthesizing capability, and its generally thick-walled tracheids with their abundant bordered pits as evidence for greater stem strength and hydraulic conductivity, *A. semicircumtrachea* appears to have attained a level of physiological fitness exceeding that of any precedent or antecedent conifer. However, excepting the remote possibilities that *A. semicircumtrachea* has affinity with Ginkgoales or *Juniperus*, there is no substantial evidence in the fossil record for the unique wood anatomical traits of *A. semicircumtrachea* having persisted through either anagenesis or cladogenesis, and thus it appears probable that *Arboramosa semicircumtrachea* n. gen. et n. sp. was a short lived species.

CONCLUSIONS

The holotype of a new genus and species of tree named *Arboramosa semicircumtrachea* from Petrified Forest National Park, Arizona, U.S.A., is a genetic anomaly of the Late Triassic Period. The fossil may also be indicative of a new but transient family because its spiralling branch junctions are unique, the first such to be clearly documented in the Mesozoic. The abundant presence of semi-circular tracheids with one straight but diagonally oriented wall, as seen in cross sections, is an entirely novel feature captured in the name of this new species. The nature of the bordered pits, manifesting on the one hand rigid intrinsic regulation of size and vertical placement yet, on the other, little or no control of placement around the circumference, is evidently unprecedented in the fossil record.

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